Muscle Function *in vivo*: A Comparison of Muscles used for Elastic Energy Savings versus Muscles Used to Generate Mechanical Power

ANDREW A. BIEWENER

Department of Organismal Biology and Anatomy, The University of Chicago, Chicago, Illinois 60637

SYNOPSIS. The function of muscles used to generate force economically and facilitate elastic energy savings in their tendons is compared with muscles that function to produce mechanical power. The underlying architectural design of the muscle and its tendon (if present) dictate much of their functional capacity and role in animal locomotion. Using methods that allow direct recordings of muscle force and fiber length change, the functional design of muscle-tendon systems can now be investigated *in vivo*. These studies reveal that, in the case of wallaby hindleg muscles, the fibers can maintain sufficient stiffness during tendon stretch and recoil to ensure useful elastic energy recovery and savings of metabolic energy. In the case of the pectoralis muscle of pigeons, although isometric or active lengthening of the muscle's fibers may occur late in the upstroke of the wing beat cycle to enhance force development, the fibers shorten extensively during the downstroke (up to 35% of their resting length) to produce mechanical power for aerodynamic lift and thrust. Oscillatory length change, with force enhancement during active lengthening may be a general feature of muscles that power aerial and aquatic locomotion. Similarly, force enhancement by active lengthening is likely to be important to the design and function of muscles that primarily generate force to minimize energy expenditure/unit force generated, as well as for elastic energy savings within a long tendon. Architectural features of muscle-tendon units for effective elastic energy savings, however, are likely to constrain locomotor performance when mechanical work is required, as when an animal accelerates, either limiting performance or requiring the recruitment of functional agonists with greater mechanical power generating capability (i.e., longer fibers).

Muscles generate the forces needed to produce and control the movement of animals. In the process of doing so, muscles may shorten to produce power by performing mechanical work, absorb energy by lengthening to do negative work, or generate force isometrically either to stabilize joints or, in combination with tendons, to store and recover elastic strain energy. In this paper, I compare the functional roles and structural design of two vertebrate muscle systems, the pectoralis of a pigeon (*C. livia*) and the hindlimb leg muscles of a moderately large hopping marsupial, the tammar wallaby (*M. eugenii*). These two sets of muscles, and the locomotory mechanisms which they power, offer contrasting designs that highlight differences of muscle architecture in relation to physiological and locomotor function.

Classical studies of isolated muscle have described well the quasistatic force-velocity and force-length relationships of skeletal muscle (Hill, 1970; McMahon, 1984). These relationships provide a guide for interpreting the physiology and design of muscles; however, the conditions under which muscles act during functional activities are considerably less well known.

The oscillatory movements of an animal's limbs and body require that many muscles, such as those which power the flight of birds and insects, or the swimming of fish, must develop force dynamically in a time-dependent fashion. Such movements function to accelerate and decelerate the mass of the body and limb segments in order to generate thrust against an external fluid medium. In these cases, muscle con-
traction often involve active lengthening and shortening phases of changing velocity within a given cycle of muscle activation. The timing and duration of muscle activation relative to lengthening and shortening can have a considerable effect on muscle power output and efficiency, as shown by in vitro studies of muscle work (Altringham and Johnston, 1990; Barclay, 1994; Johnston, 1991; Josephson, 1985, 1989). Muscles that power ballistic movements, such as the jump of frogs (Lutz and Rome, 1994; Marsh and John-Alder, 1994), or the jetting locomotion of scallops (Marsh et al. 1992), must also contract under time- and force-varying conditions.

The contractile function of muscles used in terrestrial locomotion, on the other hand, is more complex. Many limb muscles that contract to move limb and body segments likely involve dynamic changes in muscle force relative to fiber length change. Other muscles, however, likely contract with little change in length, functioning in combination with their tendons much like springs in terrestrial bouncing gaits, such as hopping, trotting or running (Alexander, 1988; Cavagna et al., 1977). Muscle function during terrestrial locomotion in vertebrates has had a long history of study, focusing mainly on the mechanical, physiological and neural requirements of motor function in mammals [see Burke (1978) and Loeb and Gans (1986) for review]. More recently, these investigations have begun to use methods that allow the direct recording of muscle force (Biewener et al., 1988; Gregor et al., 1988; Griffiths, 1989; Herzog et al., 1994; Walmsley et al., 1978) and length change (Griffiths, 1991), in combination with recordings of neural activation (Loeb and Gans, 1986), to study muscle function during in vivo activity and, therefore, are amenable for interpreting the dynamic function of muscles in the context of their classical quasistatic properties.

Fiber architecture plays a crucial role in determining the functional capacity and operating length range of a muscle, given that the force which a muscle can develop is largely proportional to its fiber cross-sectional area [under isometric conditions having a maximum of about 180 to 250 kPa (10 kPa = 1 N/cm²; Biewener et al., 1988; Close, 1972; Ettema et al., 1992; Perry et al., 1988; Wells, 1965)] and varies with changes in sarcomere length. As with studies of locomotor force and kinematics, the functional implications of muscle architecture have also had a long history of study (e.g., Gans and de Vree, 1987; McClearn, 1985; Spector et al., 1980). Muscles having long fibers with a more parallel architecture can be expected to function to produce movement and generate mechanical power by shortening with relatively large amplitude displacements. Muscles having short, pennate fibers are better designed to generate force with limited length change. When attached to the skeleton via a long tendon, these muscles can be expected to function as force generators for elastic strain energy storage and recovery within the tendon.

The architectural design features of muscles and muscle-tendon systems can be linked with their quasistatic force-velocity and force-length properties to delineate two general themes of muscle function: force generation versus mechanical power output. These functional schema, in turn, can be linked to the locomotory mechanisms that rely on their use and the media in which they most commonly apply (Fig. 1). Force generation for tendon elastic energy savings generally involves muscles that operate isometrically or on the steeply rising, lengthening portion of their force-velocity curve. By generating force isometrically, or while actively lengthening, these muscles also likely enhance their economy (metabolic energy expended/force generated). On the other hand, muscles that mainly function to generate mechanical power must operate on the shortening portion of their force-velocity curve. These muscles, therefore, generate less force/fiber and expend more metabolic energy/force. Within this framework, I contrast the functional design of the pigeon (Columbia livia) pectoralis during flight with the tammar wallaby (Macropus eugenii) plantaris and gastrocnemius during hopping locomotion.

METHODS

Muscle fiber length measurements

In two sets of experiments, the pectoralis of Silver King pigeons (n = 5, body mass
IN VIVO MUSCLE FUNCTION DURING LOCOMOTION 705

Muscle-tendon Springs
(terrestrial "bouncing" gaits)

- hop
- trot / run
- gallop

Muscle Power
(fluid propulsion & acceleration)

- flight
- swimming (jetting)
- jumping

LOCOMOTOR ACTIVITIES

ARCHITECTURE

- pennate, short fibers
- long, thin tendons

PROPERTIES

- maximize force
- high stress (strain)
- elastic energy storage

\[ U \alpha E^2 \]

(Quasistatic Contractile Properties)

Muscle-tendon Springs

Muscle Power

range: 520 to 630 g) and the gastrocnemius and plantaris muscles within the hindleg of tammar wallabies (n = 4, body mass range: 3.42 to 5.40 kg) were instrumented with 2.0 mm disc-shaped (SL5-2) sonomicrometry electrodes (Triton Technology, Inc.). All animals were fully anaesthetized (pigeons: 20 mg/kg Ketamine and 2 mg/kg xylazine; wallabies: isofluorane) prior to sterile surgery to implant the recording transducers. All experimental and surgical procedures were reviewed and approved by institutional animal care and use committees.

Prior to surgical implantation, the electrodes were epoxied to a thin (0.2 mm diameter) stainless steel support holder (Fig. 2A), designed to allow the electrodes to be anchored into position within the muscle by suture ties (4-0 silk) made through a pair of loops at the muscle’s surface. Electrode orientation was adjusted to match the muscle fibers’ pennation angle by bending the arm of the holder. The electrodes were implanted approximately five millimeters beneath the surface of the muscle by puncturing the muscle’s outer fascia with small sharp pointed scissors, opening up a space parallel to the muscle’s fibers for insertion of the
A. Wallaby: lateral gastrocnemius (unipennate)

sonomicrometer disc electrodes:
- piezoelectric film & epoxy lens
- wire support holder
- lead wires

B. Buckle Calibrations

<table>
<thead>
<tr>
<th>Muscle-Tendon Force</th>
<th>Force (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>100</td>
</tr>
<tr>
<td>2.0</td>
<td>200</td>
</tr>
</tbody>
</table>

\[ \text{GASTROCNEMIUS} \]

\[ \text{PLANTARIS} \]

C. DPC-SG

\[ \text{DPC Strain Gauge (v)} \]

<table>
<thead>
<tr>
<th>Force (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>10</td>
</tr>
<tr>
<td>20</td>
</tr>
<tr>
<td>30</td>
</tr>
</tbody>
</table>

\[ \text{DPC Strain Gauge (v)} \]
electrode. In addition to securing the two stainless steel loops of the holder, the incision through the muscle's fascia was also sutured closed after implanting the electrode to help secure its position within the muscle. Electrode position and fiber alignment were verified post-mortem. A single pair of electrodes were implanted into the bellies of the lateral gastrocnemius (unipennate, mean fiber angle: 28°) and plantaris (multipennate, mean fiber angle: 36°) muscles of the tammar wallabies. Because of its easier access, two pairs of electrodes were implanted into the sternobrachial portion of the pectoralis muscle of the pigeons in order to evaluate regional differences in fiber length change (Fig. 2C). At its superficial surface, the fibers of the pectoralis run parallel to each other, facilitating implantation and accurate alignment of the electrodes to the fibers.

Sonomicrometry recordings of length change are based on measurements of the ‘transit time’ of a 5 MHz sound pulse transmitted from an emitting to a receiving piezoelectric crystal (forming an electrode pair). A value of 1,540 ms⁻¹ (Goldman and Richards, 1954; Hatta et al., 1988) was used for the speed of sound transmission in vertebrate skeletal muscle, which requires a +2.7% correction of the Triton 120.2 Sonomicrometer’s length calibration. Length recordings were also corrected for a 5 msec phase delay introduced by the sonomicrometer’s low pass filter (Marsh et al. 1992) and a +0.74 mm offset due to the faster velocity of sound moving through the lens of each electrode. The possibility that changes in muscle density during contraction might alter the speed of sound transmission and hence, the calibration of length, has been found to be small (<5% worst case; Griffiths, 1987; Hatta et al., 1988) and thus, were ignored. Crystals were spaced 12 to 15 mm along the fibers to help ensure reliable recordings of length change.

Muscle force recordings

In the case of the wallabies, “E”-shaped stainless steel buckle transducers were surgically attached to the plantaris and gastrocnemius tendons (see Biewener and Baudinette, 1995 for details). The buckles were spaced along the tendons so that the central force-transducing arm of each was free from contact with the adjacent transducer (Fig. 2B). Each transducer was calibrated before and after its use on a nylon cord to verify that no change in sensitivity occurred during the experimental period.

In the case of the pigeons, a single-element metal foil strain gauge (FLE-1-11, Tokyo Sokki Kenkyujo) was surgically bonded to the dorsal surface of the deltopectoral (DPC) crest of the humerus (Fig. 2C), allowing the use of the DPC as ‘skeletal force transducer’. The ventral surface of the DPC forms the insertion site of the pectoralis muscle, the major wing depressor responsible for lift and thrust production during flapping flight. By bending the DPC downward, force exerted by the pectoralis can be monitored by tensile strain developed in the dorsal surface of the DPC perpendicular to the humeral shaft (see Biewener et al. 1992 and Dial and Biewener, 1993 for details).

Following completion of the in vivo recordings, the wallaby tendon buckle and pigeon DPC strain measurements were calibrated to muscle force by means of in situ calibrations of each type of transducer. Dynamic calibrations of the transducers (force buckle or DPC strain) were obtained by means of tensile loads applied directly via the tendon or the pectoralis muscle using an isometric force transducer of known sen-
sensitivity. Regressions of force vs. voltage output of the DPC strain gauge and buckle transducer (Fig. 2B, C) yielded calibrations for the rise and fall in force. Typically, these two slopes differed by <5%, and an average slope was used for the calibration of force. Correlation coefficients greater than 0.95 were obtained for all regression calibrations, with 95% confidence intervals being <4% of the regression slope.

Electromyography recordings

Electromyographic (EMG) recordings of muscles were made using fine wire (silver insulated 0.1 mm O.D., California Fine Wire) bipolar hook electrodes, having 1 mm bared ends with a 3 mm spacing between electrode tips, that were twisted along their length (Loeb and Gans, 1986). The EMG electrodes were inserted using a 23-gauge hypodermic needle at a shallow oblique angle parallel to the muscle's fascicles in locations adjacent to the sites of the sonomicrometry length electrodes and secured with 4-0 silk suture at their exit point from the muscle fascia.

RESULTS AND DISCUSSION

In vivo muscle force and fiber length recordings

Figures 3 and 4 show representative recordings made of in vivo force and muscle fiber length change in a wallaby during steady speed hopping at 4.5 ms⁻¹ (stride frequency: 3.5 Hz) and in a pigeon during slow level flight (approximately 6 ms⁻¹; wing beat frequency: 9 Hz). Most of the change in fiber length within the plantaris and lateral gastrocnemius muscles of the wallaby occurs during the swing phase of the stride. In contrast, little change in length occurs while the limb is in contact with the ground when the muscles generate force. Fiber length changes never exceeded ±2% (±0.5 mm) in the plantaris and averaged ±6% (±2.2 mm) in the lateral gastrocnemius. (Muscle fiber length changes were referenced to the resting length of the fibers recorded when the animal was anesthetized prior to tendon force calibration). Typically, however, fiber length changes were < ±3% in the lateral gastrocnemius when force development was greater than 33% of maximum (Biewener and Baudinette, 1998). Forces developed by the two muscles, which act as agonists to extend the ankle, were generally comparable, increasing with increased hopping speed from 2.5 to 6.5 ms⁻¹. When normalized for their fiber cross-sectional area, maximal stresses ranged from 130 to 230 kPa in the gastrocnemius and 160 to 250 kPa in the plantaris (Biewener and Baudinette, 1995). However, because of its smaller (13%) cross-sectional area, elastic energy savings within the gastrocnemius tendon was nearly as great as savings in the much longer plantaris tendon (41% vs. 47% of total elastic recovery; the tendon of flexor digitorum longus contributed the remaining 12%).

In contrast to the relatively small fiber length changes observed in the hindlimb muscles of tammar wallabies during hopping, fiber length changes are much greater fractions of resting fiber length in the pectoralis of a pigeon during flight (resting length of the pectoralis was determined at the end of flight sequences when the animal was resting on the perch with its wing held folded against its side). As anticipated, the pectoralis fibers are stretched during the upstroke and subsequently shorten during the downstroke (Fig. 4), exhibiting a skewed sinusoidal oscillatory pattern of length change. The rate of stretch during the upstroke occurs at nearly twice the rate of fiber shortening during the downstroke (on average fiber shortening represented 63% of the wing stroke cycle and fiber shortening represented 37%). By shortening during the downstroke, the pectoralis performs considerable positive work necessary for aerodynamic lift and thrust. Overall fiber shortening within the anterior and posterior sites of the pectoralis ranged from 30 to 36% of resting length. This was achieved by an initial 18 to 22% stretch of the fibers (from their rest length) during the upstroke and a subsequent net fiber shortening of 10–16% (see Fig. 5).

Timing of muscle activation

In both sets of muscles, neural activation of the muscle, determined by the onset EMG activity, precedes force development by a considerable period (Figs. 3, 4). In the
Wallaby hopping: 4.5 m/s

**Fig. 3.** Representative force and fiber length recordings obtained from the plantaris and (lateral) gastrocnemius muscles of a tammar wallaby hopping at 4.5 m sec⁻¹. Four successive strides are shown. Solid bars indicate the periods of electromyographic (EMG) activity recorded from each muscle. Vertical arrows indicate the onset of stance and swing phase for the second hop. Thin vertical lines at mid-stance show that fiber length change within both muscles is small during the development of force.

Wallaby plantaris and gastrocnemius, activation occurs with a phase advance (relative to cycle period) of 17% (49 msec) and 14% (40 msec) respectively. In the pigeon pectoralis, the phase advance is greater: 29% (34 msec). Activation also ends well before the cessation in muscle force. In the case of the wallaby muscles, EMG duration extends through 70 to 80% of force development; however, in the pigeon pectoralis it ceases about half way through force development (55%), nearly coincident with the timing of peak force development. The earlier onset and offset of neural activation in the pigeon pectoralis relative to the timing of force development corresponds with the much higher operating frequency of this muscle, which requires rapid force development and relaxation. For muscles that function to generate positive power under conditions of rapid oscillatory length change, phase advance of muscle activation is essential for effective force development prior to the shortening phase of the cycle, when positive mechanical work is performed (Altringham and Johnston, 1990;
Pigeon level flight: 6 m/s

Fig. 4. Representative force and fiber length recordings obtained from anterior and posterior sites of the pectoralis muscle of a Silver King pigeon during level flight at approximately 6 m sec⁻¹. Four successive wing beat cycles are shown. Solid bars denote the periods of EMG activity recorded from the muscle. Vertical arrows indicate the onset of wing downstroke and upstroke for the second cycle. Note the brief period of active lengthening of the pectoralis at the onset of force development near the end of the upstroke.


Wallaby muscle force-length behavior

When in vivo force is plotted against fiber length change, the force-length behavior and work production of the muscles can be compared for these two contrasting locomotor activities (Fig. 5). As expected from the small length changes observed during limb support, the lower leg muscles of the wallaby hindlimb exhibit isometric behavior, the pigeon pectoralis describes a broad counterclockwise loop indicative of considerable positive mechanical work.

Fig. 5. Graphs of the force-length behavior of the gastrocnemius and plantaris muscles of two wallabies during steady speed hopping compared with similar graphs for the anterior and posterior sites of the pectoralis of two pigeons during level flight. All graphs are scaled to a 45% range of fascicle length along the abscissa. The solid bar showing ±5% length change applies to all graphs. Heavy arrowheads denote the rest length of the muscle fascicle. The timing of swing (S₁) and stance (S₂) for the wallaby and upstroke (U) and downstroke (D) for the pigeon is shown. Lighter arrows show the path of length change during force development. The net mechanical work performed/cycle is also shown for each graph. Whereas the plantaris and gastrocnemius muscles exhibit isometric behavior, the pigeon pectoralis describes a broad counterclockwise loop indicative of considerable positive mechanical work.
(plantaris) or nearly isometric (lateral gastrocnemius) behavior during hopping. In the case of the plantaris, no 'work loop' (area formed during the rise and fall in muscle force) is formed by the muscle's fibers, indicating that the net work done by the muscle is negligible (<±25 mJ). Greater length changes are observed in the lateral gastrocnemius fibers; however, the work loops generated by this muscle (whether counterclockwise: positive work, or clockwise: negative work) during limb support are generally narrow. Net work produced by the lateral gastrocnemius (<±220 mJ), though small in comparison with the amount of strain energy recovered via its tendon (1600 mJ at 5.5 ms⁻¹; Biewener and Baudinette, 1995) (see also Fig. 6), is substantially greater than that of the plantaris. The main function of these two muscles therefore is to generate force economically, facilitating tendon stretch and strain energy recovery during hopping.

Previous work (Griffiths, 1989) based on in situ measurements of the medial gastrocnemius had suggested the possibility that the hindlimb muscles of wallabies (and possibly, kangaroos) are not stiff enough to maintain their length for effective strain energy storage in the tendons. However, the in vivo force-length data shown here demonstrate that this is not the case. Following force development and tendon stretch during limb support, subsequent tendon recoil is never associated with muscle fiber lengthening as force falls. Thus, strain energy stored within the tendon is usefully recovered to facilitate the elastic rebound of the wallaby’s body during the hop, rather than to cause the muscles’ fibers to be stretched during tendon recoil, dissipating the stored strain energy. The much lower amount of energy recovered by the turkey gastrocnemius tendon is due to the fact that most of its free length is calcified and too stiff to store significant strain energy. Strain energy storage occurs mainly within the aponeurosis.

The amount of strain energy recovered in the three principal hindlimb tendons combined (plantaris, gastrocnemius and flexor digitorum) represents 25% of the metabolic energy expended by the wallaby hopping at 6.0 ms⁻¹ (Baudinette et al., 1992). If the maximum efficiency of a muscle performing mechanical work via aerobic glycolysis is assumed to be 0.25 (Cavagna et al., 1977; Hill, 1970), a 25% savings (20 J) in metabolic energy (80 J) indicates that if the muscles had to do all of the work recovered by elastic savings, the tammar wallaby’s metabolic cost of hopping would be doubled at 6 ms⁻¹ (20 J/0.25 = 80 J; which would increase the total energy cost to 160 J). The energy savings by these three tendons, therefore, explains nearly all of the savings needed for moderate to large macropodids to be capable of hopping at faster speeds with little or no increase in metabolic energy expenditure (Baudinette et al., 1992; Dawson and Taylor, 1973).

**Economy of muscle force generation**

Because of the force-velocity relation, skeletal muscles can generate a given level of force with fewer fibers when contracting
isometrically versus when they shorten. Recruitment of active muscle fibers for force generation can be reduced further if a muscle is stretched, as it develops force, thereby operating on the steep lengthening portion of its force-velocity curve (Fig. 1). Presumably by contracting isometrically, or with active stretch, the metabolic cost for generating force is also reduced because fewer fibers are activated. Thus, the design and contractile function of the tammar wallaby hind leg muscles would appear to provide for economical force generation. The fact that the tammar wallaby plantaris and gastrocnemius muscles generate in vivo stresses as high as 250 kPa is consistent with their contracting at or above their maximum isometric capacity.

Economical force generation has also been observed in the gastrocnemius muscle of running turkeys (Roberts et al., 1997) using methods analogous to those described here. Similar to the wallaby plantaris and gastrocnemius muscles during hopping, Roberts et al. found that fiber length change of the turkey medial gastrocnemius was less than 7% during limb support, allowing the muscle to generate force nearly isometrically while doing only a modest amount of work. Tendon energy storage and recovery accounted for more than 60% of the work of the muscle-tendon unit during level running. In comparison (Fig. 6), tendon strain energy recovery in the wallaby accounts for nearly all (92–97%) of the net work performed by the plantaris and gastrocnemius muscle-tendon units (Biewener and Baudinette, 1998).

**Pigeon pectoralis force-length behavior**

In contrast to the narrow or non-existent work loops of the wallaby gastrocnemius and plantaris muscles (Fig. 5A), the pigeon pectoralis exhibits large counter-clockwise, positive work loops during level flight (Fig. 5B). In most instances, a small degree of active stretch of the muscle's fibers is observed late in the upstroke. Otherwise, force generally develops isometrically until the end of the upstroke and subsequently shortens during the downstroke to produce considerable work. Work per cycle by the pigeon pectoralis averaged 11.7 J/kg (muscle mass) during level flight compared with 7.1 J/kg by the wallaby gastrocnemius and only 1.0 J/kg by the plantaris during steady speed hopping at 5.5 ms⁻¹ (Fig. 6). In general, work done by fibers in the posterior portion of the pectoralis was greater than that performed by the more anterior fibers due to their greater percentage change in length. Nevertheless, the timing of muscle fiber shortening and lengthening (Fig. 4) at these two locations within the muscle were generally quite similar (<2 msec difference).

The in vivo work loops described by the pectoralis muscle during steady level flight are similar in shape to those which have been obtained based on in vitro preparations of muscles performing work when subjected to sinusoidal length changes (Altringham and Johnston, 1990; Johnston, 1991; Josephson, 1985; Rome et al., 1993; Stevenson and Josephson, 1990). Under these conditions, a gradual decline in force output occurs during the shortening phase of the cycle. While the overall magnitude of fiber length change in the pectoralis closely matches that estimated from wing kinematics (based on measurements of shoulder elevation/depression and muscle mechanical advantage), the shape of the work loop determined in vivo differs from that estimated from wing kinematics (Dial and Biewener, 1993). Kinematic estimates of fiber length change fail to show the shortening related decline in force evident from the in vivo sonomicrometry measurements. As a result, the amount of work performed by the pectoralis is likely less (about 10 to 15%) than that which we have estimated previously.

The differing roles of the wallaby hind leg muscles versus the pigeon pectoralis are clearly based on a comparison of their in vivo force-length behavior. Whereas the wallaby gastrocnemius and plantaris function to generate force economically and facilitate strain energy storage and recovery in their long tendons, the pigeon pectoralis operates on the shortening side of its force-velocity curve in order to generate mechanical power (Fig. 1). Consequently, the forces developed by the pigeon pectoralis are much lower, for its size (peak muscle stress-
es range from 54 to 76 kPa for level flight to take-off performance; Dial and Biewener, 1993), than those developed under the more nearly isometric or lengthening contractile conditions of the wallaby plantaris and gastrocnemius muscles (130–250 kPa).

Muscle-tendon architecture and contractile function

These differences in contractile function are also linked to differences in the fiber architecture of these muscles. Although tammar wallabies exceed Silver King pigeons by more than 7-fold in body mass, the mass of the pigeon pectoralis is greater than that of the wallaby gastrocnemius and plantaris muscles combined (Table 1), emphasizing the central role of the pectoralis as the main power generating muscle of flight. Indeed, the pectoralis muscles constitute 18% of the pigeon’s total body mass, and in other avian species can represent as much as 25% of body mass (Greenewalt, 1975). In addition, the average fascicle length of the pigeon pectoralis is 3.3-fold greater than that of the wallaby plantaris and gastrocnemius. The long length of its fascicles and the absence of an ‘in series’ tendon is clearly related to the pectoralis’ function to produce positive mechanical power by shortening over a considerable range of length (18 to 25 mm). In aerial flapping flight, this mechanical power is transformed to aerodynamic lift and thrust by means of extensive wing motion at the shoulder (humeral elevation/depression ranges from +80° to −20°; Dial et al., 1988). In contrast, motion of the wallaby distal limb segments is much smaller during hopping (<50° at the ankle and <25° at the metatarsophalangeal joint; Biewener and Baudinette, 1995), consistent with the primary role of the muscles being to generate force rather than movement. Indeed, most of the angular excursion of the wallaby ankle and metatarsophalangeal joints is accounted for by stretch and recoil of the muscles’ tendons (plantaris: 91–95% and gastrocnemius 51–81% of total muscle-tendon length). By having shorter pennate fibers, the muscles may also able to generate this force more economically, reducing the amount of energy consumed per unit force (Roberts et al., 1997).

The design for effective force generation (force/unit volume of muscle) with economical energy utilization in the hindlimb muscles of saltatory macropods, however, is certainly not extreme by mammalian standards (Alexander et al., 1982). In particular, fibers within distal limb muscle-tendon units of moderate to large ungulates (Table 1) are extremely short, often being two orders of magnitude less than the length of their tendons. Given that normal functional strains within the tendons are likely to be within the range of 2 to 4% [based on unpublished observations for estimated tendon stresses in horses and measurements made in tammar wallabies (Biewener and Baudinette, 1995)], elastic deformations of 20 to 25 mm, or more, are likely to occur within the tendons of these short pennate fibered muscles. With such short fibers, the capacity of the muscle to control distal limb segment position via a long tendon is virtually nil. Almost certainly, selection has favored effective and economical force generation by these muscles and elastic storage and recovery via their tendons. Indeed, the muscle fibers of the plantaris (or superficial digital flexor) of horses, camels, and other large ungulates are vestigial, essentially having been transformed into a long elastic ligament (850 mm in length for a 300 kg horse). A similar loss of muscle fibers and contractile function has also occurred in the suspensory ligaments of the carpus and tarsus of these animals (Table 1).

These evolutionary changes in muscle-tendon design represent extreme examples of selection for reducing energy expenditure and facilitating elastic savings by means of a bouncing terrestrial gait. If economy of force transmission and elastic storage can be optimized by eliminating muscles, what constraints limit the evolution of passive elastic elements, such as ligaments? The most obvious tradeoff is the need for control of position and movement (Rack and Ross 1984). Economical travel is advantageous, but only if adequate control for balance and maneuvering is maintained. In nearly all cases in which selection
Table 1. Fiber architecture of various muscles in relation to their likely role for economical force production (F) and elastic savings (ES) versus generating mechanical power (P). Elastic deformation (ΔL) of tendon is based on a locomotor strain of 3%.

<table>
<thead>
<tr>
<th>Animal (body mass)</th>
<th>Muscle</th>
<th>Mass (g)</th>
<th>Fascicle length (mm)</th>
<th>Tendon length (mm)</th>
<th>Tendon elastic AL (mm)</th>
<th>tFunction</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horse (270 kg)</td>
<td>Plantaris</td>
<td>10</td>
<td>2.5</td>
<td>830</td>
<td>24.9</td>
<td>ES</td>
<td>Biewener (unpublished data)</td>
</tr>
<tr>
<td></td>
<td>Gastrocnemius</td>
<td>1,107</td>
<td>39</td>
<td>340</td>
<td>10.2</td>
<td>ES, F (&amp;P)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tarsal interosseous</td>
<td>**</td>
<td>**</td>
<td>335</td>
<td>10.1</td>
<td>ES</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flexor digitorum superficialis</td>
<td>703</td>
<td>6</td>
<td>620</td>
<td>18.6</td>
<td>ES, F</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(humeral head)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flexor digitorum profundus (radial/ulnar head)</td>
<td>206</td>
<td>60</td>
<td>625</td>
<td>18.8</td>
<td>F (&amp;P)</td>
<td></td>
</tr>
<tr>
<td>Camel (402 kg)</td>
<td>Plantaris</td>
<td>**</td>
<td>**</td>
<td>860</td>
<td>25.8</td>
<td>ES</td>
<td>Alexander et al. (1982)</td>
</tr>
<tr>
<td></td>
<td>Gastrocnemius</td>
<td>1,172</td>
<td>50</td>
<td>550</td>
<td>16.5</td>
<td>ES, F (&amp;P)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tarsal interosseous</td>
<td>**</td>
<td>**</td>
<td>480</td>
<td>14.4</td>
<td>ES</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flexor digitorum superficialis</td>
<td>190</td>
<td>12</td>
<td>1,010</td>
<td>30.3</td>
<td>ES, F</td>
<td></td>
</tr>
<tr>
<td>Wallaby (4.8 kg)</td>
<td>Plantaris</td>
<td>24</td>
<td>16</td>
<td>300</td>
<td>9.0</td>
<td>ES, F</td>
<td>Baudinette (1995)</td>
</tr>
<tr>
<td></td>
<td>Gastrocnemius</td>
<td>27</td>
<td>17</td>
<td>165</td>
<td>5.0</td>
<td>ES, F (&amp;P)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Biceps femoris</td>
<td>84</td>
<td>54</td>
<td>0</td>
<td>0</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vastus lateralis</td>
<td>45</td>
<td>35</td>
<td>55</td>
<td>1.7</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>Pigeon (0.65 kg)</td>
<td>Pectoralis</td>
<td>58.2</td>
<td>60</td>
<td>0–44</td>
<td>0–1.3</td>
<td>P</td>
<td>Biewener, Tobalske and Corning (unpublished)</td>
</tr>
<tr>
<td></td>
<td>Supracoracoideus</td>
<td>11.1</td>
<td>23</td>
<td>93</td>
<td>2.8</td>
<td>P (&amp;F)</td>
<td></td>
</tr>
<tr>
<td>Starling (0.072 kg)</td>
<td>Pectoralis</td>
<td>5.5</td>
<td>26</td>
<td>0–25</td>
<td>0–0.8</td>
<td>P</td>
<td>Biewener et al. (1992)</td>
</tr>
<tr>
<td></td>
<td>Supracoracoideus</td>
<td>5.5</td>
<td>8</td>
<td>40</td>
<td>1.2</td>
<td>P (&amp;F)</td>
<td></td>
</tr>
</tbody>
</table>

† Functional distinction between force and power was established by the following elastic extension ratios (R_e = tendon ΔL/fiber length):
P  R_e < 0.10
P (&F)  0.10 < R_e < 0.25
F (&P)  0.25 < R_e < 0.40
F  R_e > 0.40
has favored extreme design for economical force generation and elastic savings (short, pennate fibered muscles with long tendons), agonist muscles with longer fibers are also present to provide greater control of limb position (compare, for example, the much longer fibers of the humeral head of flexor digitorum profundus versus its radial/ulnar head, as well as that of flexor digitorum superficialis, in the horse, Table 1). In addition, whereas economy of force generation and elastic savings tend to be emphasized in distal limb muscle-tendon units (which also favor a decrease in limb inertia), more proximal muscle groups (e.g., biceps femoris and vastus lateralis) generally appear well designed for adjustments in mechanical power that are likely to be important under conditions of acceleration or deceleration, and locomotion over uneven terrain.

To what extent does a muscle-tendon system designed for elastic savings constrain an animal’s ability to adjust its locomotor performance in regard to acceleration or movement over uneven terrain, which demand increased mechanical power output and control of foot position? Is an increase in locomotor power achieved by the means of recruiting differing sets of muscles in the limb, or can this be achieved by changes in the contractile function within the same set of muscles? Architectural features of muscles and their tendons suggest that tradeoffs in function exist and are likely met by the recruitment of differing groups of muscles for differing motor tasks. Future studies of muscle function under in vivo conditions of both steady and non-steady exercise, however, are needed to begin to address these questions.

ACKNOWLEDGEMENTS

I gratefully thank Russell Baudinette for making the work on wallabies possible, Ken Dial, Bret Tobalske, Doug Warwick and Will Corning for their enthusiasm and assistance in our collaborative studies of bird flight, and John Gilpin for machining the tendon buckles and helping to design and fabricate the force transducer and calibration equipment. Supported by NSF grants IIB-9306793 and IIB-9723699.

REFERENCES


Corresponding Editor: Todd Gleason